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Comments on the Relationships of the North American Cave Fishes of the Family Amblyopsidae

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INTRODUCTION

Amblyopsids are small, North American, fresh-water fishes with reduced or no eyes, a jugular vent, and troglodytic habits. Five species are currently recognized in three genera: *Amblyopsis*, *Typhlichthys*, and *Chologaster* (Woods and Inger, 1957). The present association of amblyopsids with the cyprinodontiforms dates to Starks's (1904) osteological analysis of *Amblyopsis spelaea*. When Regan (1911b) delimited the cyprinodontiforms (his Microcyprini) as a distinct order, the amblyopsids as defined by Starks were included uncritically with them, and united with the Cyprinodontiformes they have since remained, although reasons for contesting this alignment have twice appeared in the literature. Frost (1926) illustrated the differences between the otoliths of amblyopsids and those of the cyprinodontiforms proper, and Woods and Inger (1957) demonstrated that the ligamentous attachment of the shoulder girdle of amblyopsids is developed as in the esocoid *Umbra*.

The original objective of the present study was an osteological and myological comparison of the Amblyopsidae (suborder Amblyopsoidei) with the typical killifishes (suborder Cyprinodontoidei). Of many structures in the cranial and postcranial skeleton that were compared, the

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majority showed little similarity between these two groups of fishes. The need for reassessing amblyopsid relationships was thus established.

Dissections of the jaw muscles of amblyopsids revealed a condition in which a deeply situated cheek muscle of disputed homology inserts on the maxilla, and a superficial cheek muscle that regulates the cyprinodontoid maxilla is obsolescent. A similar muscle arrangement was noted previously by Eaton (1935) in the percopsiform *Aphredoderus*, and in the gadiforms *Gadus, Melanogramma,* and *Merluccius.* He commented that "*Aphredoderus* differs markedly from other perch-like fishes," and that, in the special form of its jaw muscles and in many aspects of the cranial bones, ". . . *Aphredoderus* appears to be allied to the Anacanthini." The common occurrence of this particular muscle pattern and a jugular vent in amblyopsids and aphredoderids provided the incentive for the investigation reported here.

There are numerous superficial resemblances between amblyopsids and the killifishes. These include small size, the absence of fin spines and the virtual absence of ctenoid scales, a typically truncate caudal fin and large and rather highly placed pectoral fins, and an abdominal or subabdominal position for the pelvic fins when they are present. Cyprinodontoids as a group are so diversified that the few obvious differences between them and the amblyopsids (for example, the jugular vent) were minimized in earlier classifications. Starks (1904) and Myers (1931) did call attention to several osteological differences, but these were never regarded as of more than subordinal significance. Actually, the array of osteological and other differences between amblyopsids and the killifishes is imposing, including no fewer than two dozen features of the skeleton and musculature alone. The salient characteristics of the syncranium, shoulder girdle, and caudal skeleton of amblyopsids not shared by cyprinodontoids are given extensively in table 1 and in the figures. Table 1 also includes comparisons of both cyprinodontoids and amblyopsids with *Aphredoderus*, and the number of similarities between the latter two gives support to the idea that amblyopsids and cyprinodontoid killifishes are improperly associated taxonomically.

ABBREVIATIONS OF INSTITUTIONS

A.M.N.H., the American Museum of Natural History
C.U., Cornell University, Ithaca, New York
U.F., University of Florida, Gainesville
U.M.M.Z., University of Michigan Museum of Zoology, Ann Arbor
U.S.N.M., United States National Museum, Washington, D.C.

Abbreviations Used in Illustrations

A, adductor mandibulae muscle
AAP, adductor arcus palatini muscle
ACT, actinost or radial
ART, articular
BB, basibranchial
BBP, toothed dermal basibranchial plate
BOC, basioccipital
BR, branchiostegal ray
CB, ceratobranchial
CH, ceratohyal
CL, cleithrum
CO, coracoid
CR, cranium
DN, dentary
DO, dilatator operculi muscle
EB, epibranchial
ECT, ectopterygoid
EH, epihyal
ENT, entopterygoid
EOC, exoccipital
EP, epiotic
ETH, ethmoideum
FR, frontal
G, gill plate
GH, glossohyal
GR, gill raker
HB, hypobranchial
HH, hypohyal
HYO, hyomandibular
IC, intercalar ("opisthotic")
IF, inferior pharyngeal tooth plate
IH, interhyal
IOP, interoperculum
LAP, levator arcus palatini muscle
LE, lateral ethmoid
LMS, levator maxillae superioris muscle
MET, metapterygoid
MX, maxilla
NA, nasal
OEB, outline of eyeball
OP, operculum
PA, parietal
PAL, palatine (autopalatine with or without dermopalatine)
PAS, parasphenoid
PASA, arms of parasphenoid
PB, pharyngobranchial tooth plate
PFR, prefrontal
PLS, pleurosphenoid

PMX, premaxilla
POP, preoperculum
PRO, pro-otic
PT, pterotic
PTT, posttemporal
PV, prevomer
QU, quadrate
R, median ridge on frontal
SC, scapula
SCL, supracleithrum
SG, shoulder girdle
SO, suborbital bones (including "lachrymal")
SOC, supraoccipital
SOP, suboperculum
SPH, sphenotic
SYM, symplectic
TRF, trigeminofascialis foramen
UH, urohyal

MATERIALS AND METHODS

Alizarin-glycerine skeletons, and dissections, were prepared from the following comparative materials:

Amblyopsidae
    Chologaster agassizi Putnam; U.F. No. 1436
    Chologaster cornuta Agassiz; C.U. Nos. 4089, 29911, 30140, 30716, 31770
    Typhlichthys subterraneus Girard; U.F. No. 696
    Amblyopsis spelaea DeKay; A.M.N.H. No. 20439
Aphredoderidae
    Aphredoderus sayanus (Gilliams); U.F. Nos. 1299, 8362
Brotulidae
    Monomitopus agassizi (Goode and Bean); U.S.N.M. No. 196536
Gadidae
    Microgadus proximus (Girard); A.M.N.H. No. 2740
    Microgadus tomcod (Walbaum); A.M.N.H. No. 9024
    Urophycis floridanus (Bean and Dresel); U.F. No. 2680
Ophidiidae
    Ophidion holbrooki (Putnam); U.S.N.M. No. 196539
Percopsidae
    Percopsis omiscomaycus (Walbaum); U.F. No. 8718
    Percopsis transmontana (Eigenmann and Eigenmann); U.M.M.Z. No. 98801
Umbridae
    Umbra limi (Kirtland); U.F. Nos. 1446, 8703

Numerous cyprinodontoid killifishes also were used from the author's collateral studies. Many of the distinctive features of amblyopsids and *Aphredoderus* were seen especially in *Percopsis*, *Urophycis*, *Microgadus*,

Ophidion, and *Monomitopus*. These similarities are noted in the text, figures, and the legends to the figures.

Various problems of the muscle nomenclature in teleosts are unresolved; mention is made here of those concerned with the jaw muscles innervated jointly by the facialis and trigeminus nerves. In general, in teleosts two or three sheets of cheek, or adductor mandibulae, muscles insert on the jaws, and these are usually arranged as a superficial, middle and/or in-
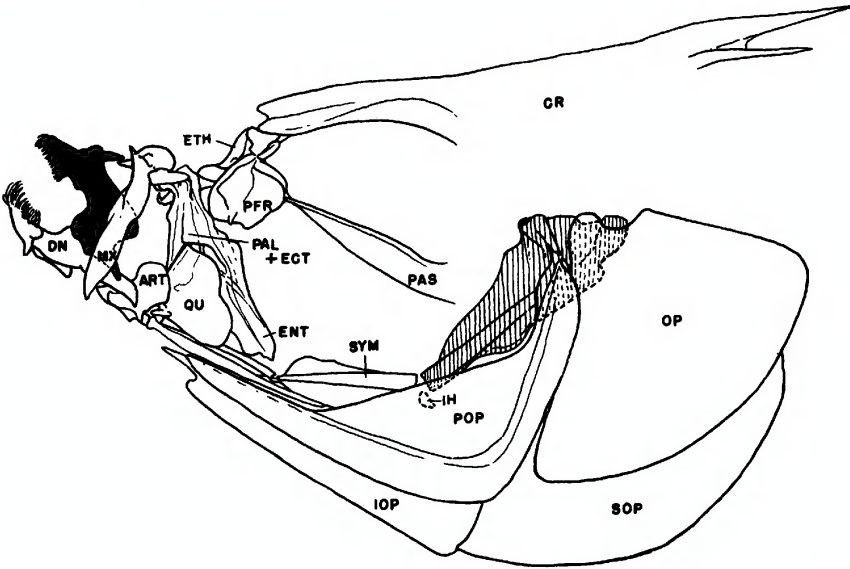

Fig. 1. Jaws, jaw suspension, and opercular apparatus of the cyprinodontoid *Xiphophorus helleri* Heckel. Note expanded lower premaxillary arm and its position between mandible and maxilla, absence of metapterygoid, absence of a foramen in the hyomandibular, absence of opercular spines. Premaxilla in solid black; hyomandibular vertically lined; interhyal (ih) dashed, as seen through preoperculum. Compare with figures 4, 5A, and 16.

ternal layer. Partly above and partly internal to the cheek muscles are two or more muscles that insert on the jaw suspension (adductor and levator arcus palatini) and on the opercular apparatus (dilatator operculi). In *Amia* still another cluster of smaller muscles arises between the adductor mandibulae and the adductor arcus palatini; this muscle, termed levator maxillae superioris, was thought to be absent as such in teleosts.

Vetter (1878), Allis (1903), Eaton (1935), and others distinguished the three levels of cheek or adductor mandibulae muscles in teleosts as A_1,

TABLE 1

Comparisons of Cyprinodontoid Killifishes with Amblyopsids and *Aphredoderus*

	Cyprinodontoidei	Amblyopsidae	*Aphredoderus*[a]
Skull (figs. 1, 2, 4, 5, 10–14, 16, 20–22, 24)			
Prevomer	Usually present, rarely toothed	Present and toothed	—
Circumorbital bones	Preorbital and postorbital members present, intervening elements absent; preorbital with small articular nubbin on medial surface	Preorbital and postorbital and two or three suborbital elements present; preorbital with long style projecting diagonally inward and backward toward prefrontal	Circumorbital series complete; preorbital as in Amblyopsidae
Frontal	Rectangular, truncate or indented rostrally, with prominent orbital and temporal divisions	Subtriangular, tapering rostrally, without prominent orbital and temporal divisions	—
Pro-otic	Joining a distinct ventral arm of parasphenoid, trigeminofascialis chamber opening ventrally, foramen for carotid artery displaced forward near ventral arm of parasphenoid	Not joining a distinct ventral arm of parasphenoid, trigeminofascialis chamber opening laterally, foramen for carotid artery immediately adjoining trigeminofascialis chamber	—
Epiotic	Usually with crests	Without crests	—
Intercalar (= opisthotic)	Minute when rarely present on exoccipital	Large, overlapping pterotic and exoccipital	Smaller, crescent-shaped, but overlapping pterotic and exoccipital
Supraoccipital	Of constant form, shaped like head of battleax	Of irregular form	—
Parietal	Present or absent, when present of variable size and shape but with long axis extending obliquely forward from supraoccipital	Present and well developed, long axis parallel with that of cranium	—

TABLE 1—(Continued)

	Cyprinodontoidei	Amblyopsidae	Aphredoderus
Posttemporal	Bifid or simple, attached to epiotic without intervening ligament; when bifid, lower arm attached to minute intercalar or to ventral portion of epiotic without intervening ligament	Incompletely bifid and attached to epiotic (dorsally) and large intercalar (ventrally) by intervening ligament	—
Supracleithrum	Small or minute, confined within dorsal tip of cleithrum	Long strut one-half to one-third as long as cleithrum	—
Otoliths	Lapilhus smaller than asteriscus	Lapillus larger than asteriscus	—
Parasphenoid	Not expanded, usually with distinct dorsal and ventral arms and constantly with median ventral keel	Greatly expanded, without distinct dorsal and ventral arms or median ventral keel	Not expanded, with ventral arms but without distinct dorsal arms or median ventral keel
Palatine	Edentulous	Distinctly toothed	—
Ectopterygoid	Coossified with palatine	Small but distinct	—
Entopterygoid	Present; edentulous	Present; edentulous	Present; with inner tooth patch
Metapterygoid	Rarely a bone in metapterygoid position that does not touch quadrate	Present	—
Premaxilla	With ascending process only; lower arm greatly expanded, not segmented, attached directly to mandible	With distinct ascending and articular processes; lower arm frequently segmented, carried on maxilla	—
Maxilla	With upper flange and deep internal hook enclosing premaxilla at base of ascending process; separated from mandible by arm of premaxilla	With large node at head and broad flange slipping under articular process of premaxilla; attached directly to mandible	—

TABLE 1—(*Continued*)

	Cyprinodontoidei	Amblyopsidae	*Aphredoderus*
Hyomandibular	Without large, window-like foramen	With large, window-like foramen	—
Operculum	Without spines, margin entire	With two dorsal and frequently one ventral spine	—
Pharyngobranchial 1	Absent	Trifid, with a few small teeth	—
Pharyngobranchial 2	Tooth bearing, consolidated with pharyngobranchials 3 and 4	Tooth bearing, consolidated with pharyngobranchial 3	—
Pharyngobranchial 4	Tooth bearing, consolidated with pharyngobranchials 2 and 3	Tooth bearing, distinct	—
Gill rakers	Simple, arranged serially	Complex, in clusters or islands of 5 to 10 minute rakers	—
Hypobranchial 1	Joining copula on 1st basibranchial	Joining copula between 1st and 2d basibranchials	—
Hypobranchial 2	Joining copula on 2d basibranchial	Joining copula between 2d and 3d basibranchials	—
Hypobranchial 3	Joining copula on or behind 3d basibranchial	Joining copula on 3d basibranchial	—
Dermal basibranchial plate	Absent	Toothed posterior remnant present	—
Shoulder girdle			
Ligamentous support	To basicranium	To 1st vertebra	—
Cleithrum	Strut-like, with expanded dorsal plate	Bow-shaped, without expanded dorsal plate	—
Scapula	Joined dorsally and anteriorly to bone of cleithrum; with recess for 2 dorsal actinosts	Embedded in cartilage; without recess for actinosts	—
Coracoid	Joined dorsally to scapula and anteroventrally to cleithrum; with recess for 2 ventral actinosts	Embedded in cartilage; without recess for actinosts	—

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TABLE 1—(*Continued*)

	Cyprinodontoidei	Amblyopsidae	*Aphredoderus*
Actinosts	4 in number; subrectangular	4 in number; dumbbell-shaped	—
Position of vent	Abdominal or subabdominal	Jugular	—
Olfactory organ	Small, not lobed	Large, lobed	—
M. adductor mandibulae (figs. 3, 6–9)	With a large external division (A_1) to lower arm of maxilla	With external division (A_1) obsolescent or absent	—
M. levator maxillae superioris (figs. 6–9)	Absent	Present anteriorly	—
Upper jaw ligaments (figs. 4–8)	Absent, or with a crosswise ligament joining both palatines	Present; a ligament joining maxilla and ethmoid crossed by one joining palatine and premaxilla	—
Caudal skeleton (figs. 17–19)	Symmetrical; an epural above and a hypural below median triangular hypural plate, all arranged around terminal half-centrum; vertebrae not upturned; no uroneural above hypural plate; last neural and hemal spines unbranched	Asymmetrical; one or two epurals and a uroneural above superior hypural plate on terminal half-centrum; a hypural element below inferior hypural plate on last complete centrum; superior hypural plate extending farther posteriad than inferior plate; terminal vertebrae usually slightly upturned; last neural spine, rarely the last hemal spine, bifid	

[a] A dash indicates no major distinction between the amblyopsids and *Aphredoderus*.
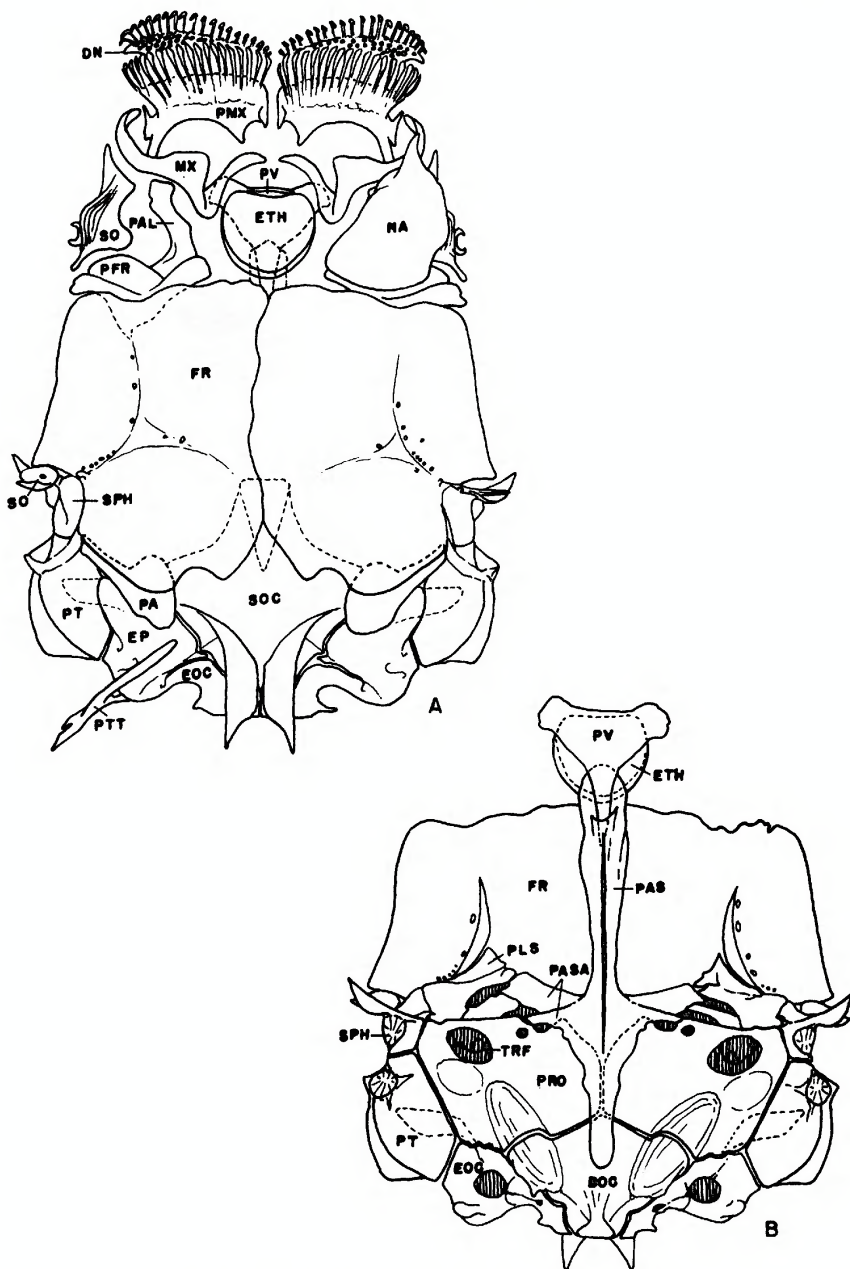
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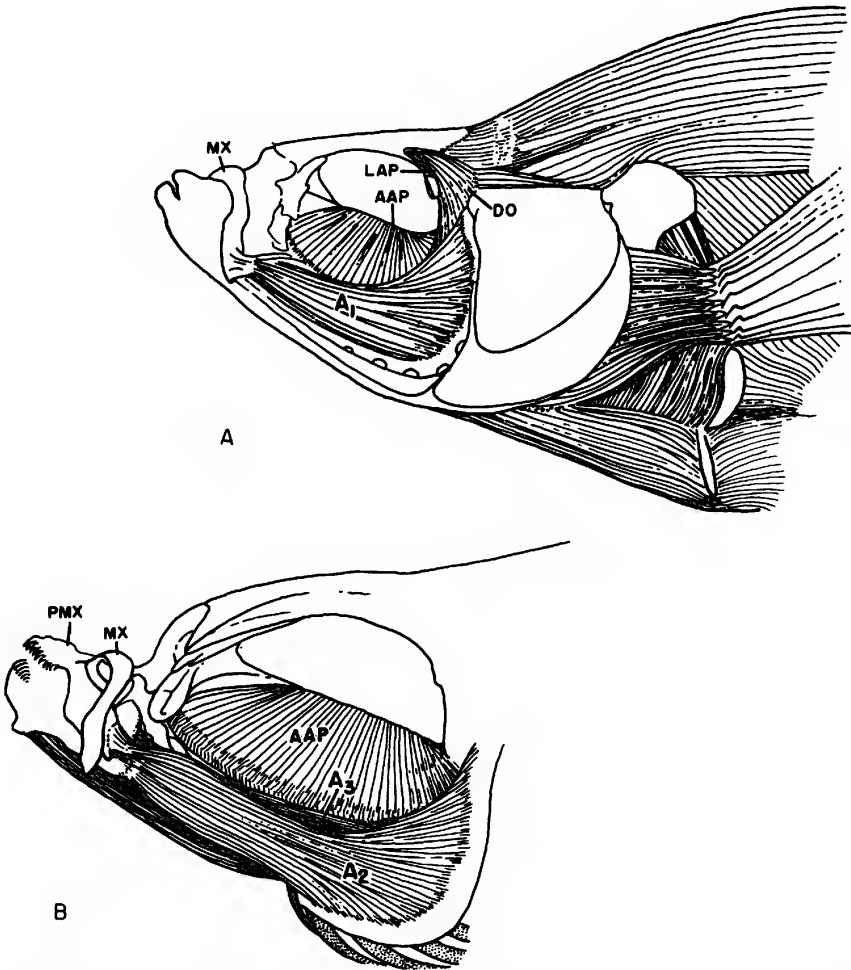FIG. 2. *Xiphophorus variatus* (Meek). A. Dorsicranium. B. Basicranium. Compare with figures 20 and 21.

Fig. 3. Jaw musculature of cyprinodontoid killifishes, semidiagrammatic, composite, based on representatives of several New World types. A. Superficial muscles of head in relation to opercular apparatus and anterior trunk muscles. B. Deeper jaw muscles; the unlabeled ventralmost muscle running forward to the lower mandible is the geniohyoideus.

A_2, and A_3, the two innermost divisions often being consolidated into a singe body, A_2A_3. In Takahasi's (1925) terminology, which is based on muscle insertion instead of origin, all cheek muscles of which the principal force is applied to the mandible, are referred to the composite A_2A_3, and all muscles affecting chiefly the maxilla to A_1.

Allis (1903) defined as t.a$_3$mx the tendon in *Scomber* that runs from the

medial surface of the adductor to the upper portion of the maxilla and arises from fascia on what he termed A_3. Takahasi, however, referred to an internal muscle in the cod occupying the position of t.a$_3$mx as A_1, because it inserts on the maxilla. The fact that the more usually inserted A_1 (A_2' of Allis, 1897; A_1 of Allis, 1903, and others) also is present in
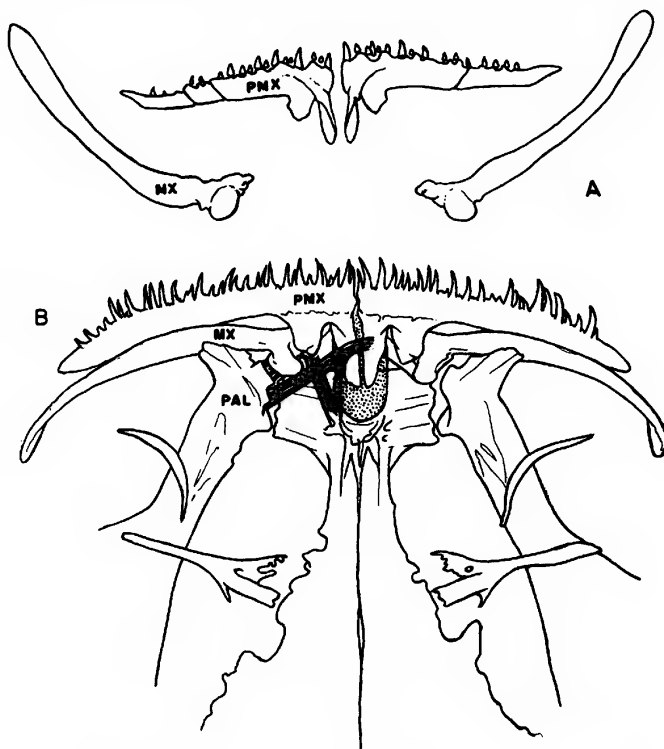
FIG. 4. Upper jaw bones of the Amblyopsidae. A. Maxilla and premaxilla of *Chologaster agassizi* Putnam. B. Upper jaw suspension of *Typhlichthys subterraneus* Girard; upper jaw ligaments are shown diagrammatically on left side. The rostral cartilage is stippled. Note segmental subdivisions of premaxilla in *Chologaster*.

Gadus and other fishes caused Takahasi to recognize two divisions of A_1: an internal or upper division ($A_{1\alpha}$) and an external or lower division ($A_{1\beta}$). A similar system was employed by Dietz (1914, 1921) and Edgeworth (1935). Eaton referred to the internal muscle corresponding with t.a$_3$mx in aphredoderids and gadids as A_3.

Another muscle of uncertain identity in the cod extends from an anterior pocket of the hyomandibular just behind the eye downward and forward

internal to the adductor mandibulae, converging on the muscle referred to by Eaton as A_3. Takahasi, in a figure, labeled this muscle as if it were a disjunct portion of the composite A_2A_3. Eaton, however, provisionally assigned it the symbol A_4, saying that it corresponds in appearance and
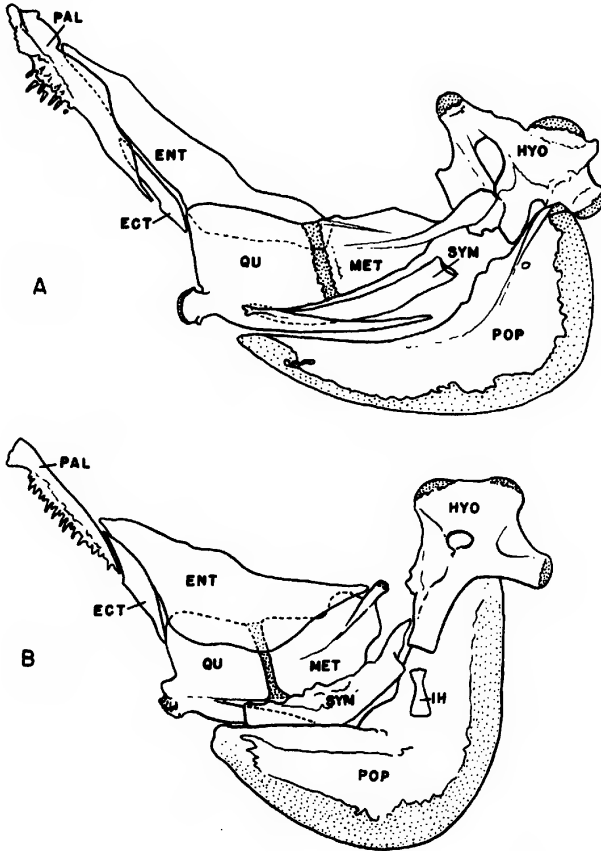

FIG. 5. Jaw suspension and preoperculum. A. Lateral view of *Chologaster agassizi* Putnam. B. Medial view of *Umbra limi* (Kirtland). Compare with figure 10.

position with a posterior division of the levator maxillae superioris (lms[1]) of *Amia*.

Actually, not only does A_4 correspond with lms[1] (lms[1,2] of Allis, 1897), but the muscle of gadids termed A_3 by Eaton ($A_{1\alpha}$ of Takahasi) bears a striking resemblance to the anterior divisions of the levator maxillae (lms[3] and lms[4]) of *Amia*. This latter muscle in *Monomitopus* and *Ophidion* is divided near its origin, in which condition it is even more suggestive of the
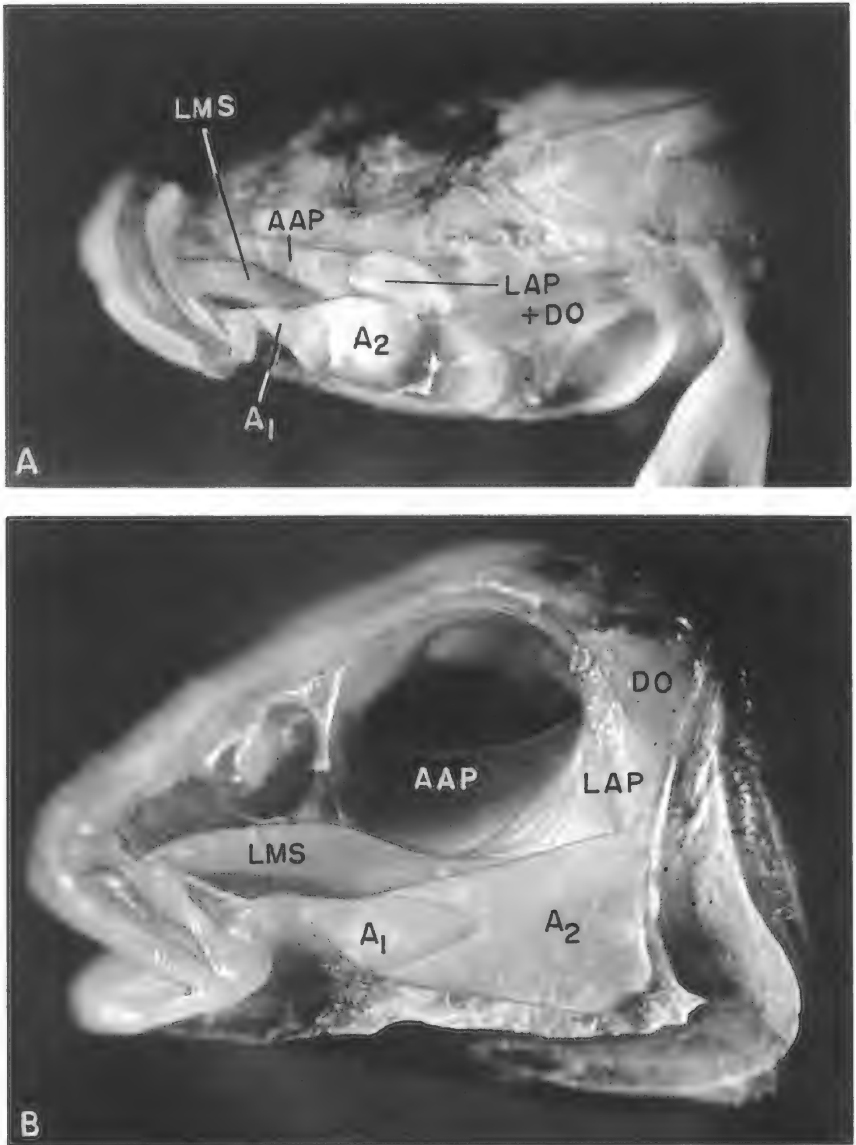
FIG. 6. Retouched photomicrographs of jaw muscles. A. *Chologaster agassizi* Putnam. The muscle labeled A_2 is probably united with the underlying A_3; it is referred to in the text as A_2A_3. B. *Percopsis omiscomaycus* (Walbaum). Compare with figures 7–9.

anterior pair of levator maxillae muscles of *Amia*. The resemblances between *Amia* and *Microgadus* in over-all architecture of the jaw muscles are such that the provisional use of the name levator maxillae superioris for these internal muscles of the cods and their allies seems justified. In *Microgadus proximus* (see fig. 7) the posterior levator maxillae superioris muscle
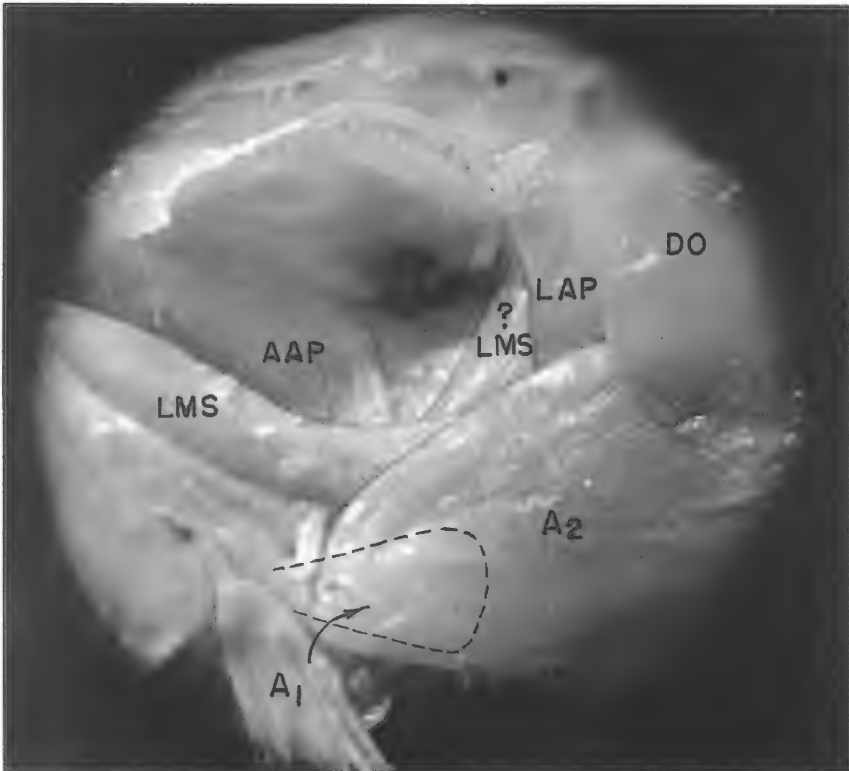
Fig. 7. Retouched photomicrograph of jaw muscles of *Microgadus proximus* (Girard). A_1 was removed to position shown; original position is indicated by arrow and dashed line. The questionable assignment of a muscle in the posterior wall of the orbit (? lms) to the levator maxillae superioris series is described in the text.

originates on a broad tendinous sheet that lies on the quadrate and metapterygoid entirely internal to the adductor mandibulae series. In this origin and in its insertion along the anterior edge of the hyomandibular this muscle, as Eaton noted, resembles lms[1,2] of *Amia*. The anterior pair of levator maxillae superioris muscles (lms[3,4]) are in some instances partly distinct, in others, completely united. They originate on an ex-

Fig. 8. Retouched photograph of the head of *Monomitopus agassizi* (Goode and Bean), with the mouth widely opened. The left cheek muscles, crossed rostral ligaments, and roofing bones have been exposed, and the eye has been removed to reveal the full extent of the upper jaw muscles.

tremely tough, flat tendon on the metapterygoid posterior to the origin of lms[1,2]. From this point they pass obliquely forward over the belly of lms[1,2] and, following the palatopterygoid, insert high up on the posterior edge of the maxilla. In *Microgadus tomcod* the situation is much the same, except that the internal division (A_3) of the adductor mandibulae muscle is better developed. In this species, the fibers of the upper posterior end of A_3 are united with those of lms[1,2], so that A_3 and lms[1,2] have the appearance of being a single muscle that originates on the hyomandibular and inserts on the mandible (see, for example, Dietz, 1921). In joining lms[1,2] in *M. tomcod*, A_3 passes underneath a portion of lms[3,4] for a short distance, thus establishing a complete depth sequence of the jaw muscles

Fig. 9. Retouched photograph of the head of *Aphredoderus sayanus* (Gilliams), with the mouth widely opened. The left cheek muscles have been exposed.

from the superficial muscles inward, as follows: A_1, A_2, $lms^{3,4}$, A_3, $lms^{1,2}$. If some consolidation in the levator maxillae series is allowed for, this sequence is essentially that illustrated by Allis for *Amia*. The innervation of these internal muscles apparently supports their identification with the levator maxilla series. Both $lms^{1,2}$ and $lms^{3,4}$, as used here, receive fibers from a branch of the maxillaris inferioris trigemini and from a branch of the facialis that follow a common course to the lms muscles, as in *Amia*. Although the posterior division of this muscle was formerly suggested as belonging to the lms series, the anterior division ($lms^{3,4}$) never was, al-

though it was assigned many names (see table of synonyms in Edgeworth, 1935). Apparently only Allis and Takahasi previously admitted the possibility that the anterior levator maxillae superioris muscles are present in some form in teleosts.

DISCUSSION

As indicated, the feature of amblyopsids that most strikingly sets them apart from the killifishes is the jaw mechanism. In killifishes the premaxilla has a direct ligamentous attachment to the lower jaw and is
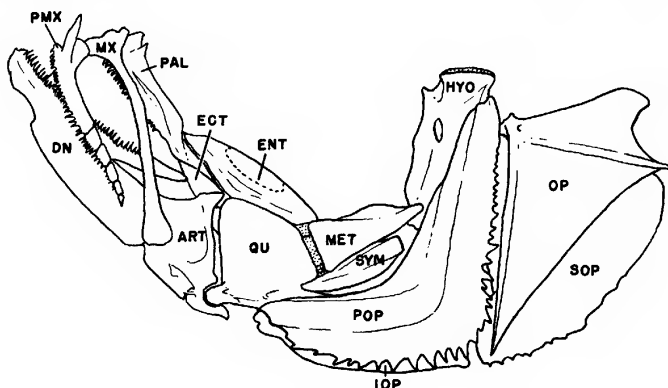

Fig. 10. Jaws, jaw suspension, and opercular apparatus of *Aphredoderus sayanus* (Gilliams). The dashed line on the entopterygoid represents the limits of a tooth patch on the medial surface. In *Percopsis omiscomaycus* the entopterygoid and palatine are without teeth. Compare with figures 4A, 5A, and 16.

sandwiched between the mandible and the maxilla (fig. 1). Its upper end is attached only to a deep internal hook of the maxilla (fig. 2A) by an elastic bed of connective tissues, although the rostral cartilage is held down by a crosswise ligament that extends between the two palatines. In some killifishes the excursion forward of the highly protrusile premaxilla is brought about directly by abduction of the lower jaw to which it is bound. Its withdrawal back to the rostrum is influenced by contraction of the distinct A_3 to the inner mandible, A_2 to the premaxilla and the coronoid process of the mandible, and by the sudden rotation of the maxilla following relaxation of a large adductor component (A_1) that inserts on the outer posterior face of the lower end of the maxilla (fig. 3A, B). The cyprinodontoid maxilla exercises principally a restraining and bracing function, as pointed out by Schaeffer and Rosen (1961).

The jaw of amblyopsids suggests at first a generalized percoid condition in which the maxilla and premaxilla are braced by a set of crossed ligaments (fig. 4). Furthermore, the premaxilla plays no direct role in upper jaw movements, because its lower end is joined only to the maxilla, the two bones being arranged in tandem and not overlapped as in killifishes. In addition to the osteological details that distinguish the amblyopsid and the cyprinodontoid upper jaw (see table 1 and figs. 1, 5A), there is a profound difference between them in the nature of the muscular control. In amblyopsids the external division of the adductor mandibulae (A_1)
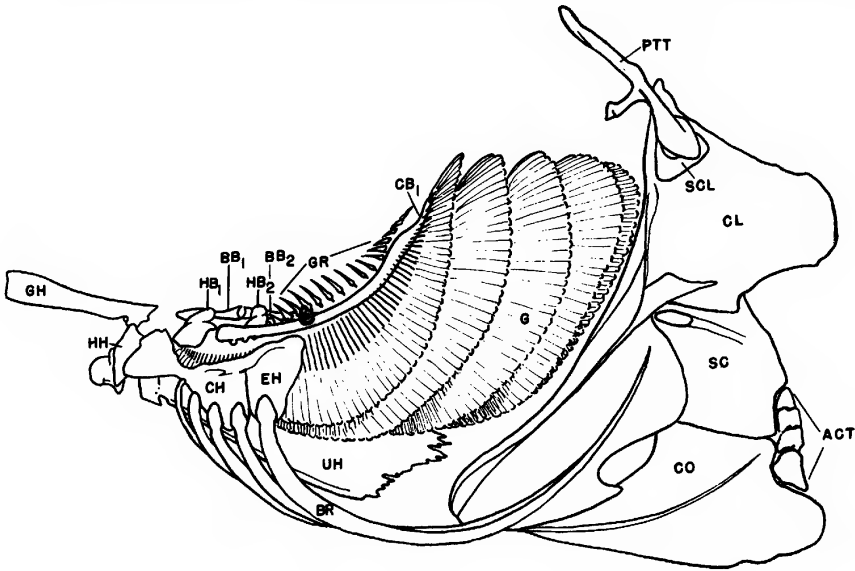
FIG. 11. Pharyngobranchial apparatus and shoulder girdle of the cyprinodontoid *Xiphophorus helleri* Heckel, lateral view. Interhyal in solid black. Compare with figures 12 and 15.

that is so important in the cyprinodontoid mechanism is obsolescent, a composite A_2A_3 inserts only on the mandible and never on any portion of the premaxilla, and maxillary control is asserted instead primarily by a levator maxillae superioris muscle (probably $lms^3 + lms^4$).

The mechanism of opening the mouth in the Amblyopsidae is essentially that described by Schaeffer and Rosen (1961) for the cod. In this system the mouth, when widely opened, is approximately circular in front outline and nearly straight down from the premaxillary to the dental symphysis in side view. When the lower jaw is abducted, the maxilla,

which is attached by ligaments near the coronoid process, is drawn downward and forward. As the maxilla rotates forward on its palatine hinge, it presses against the toothed ramus of the premaxilla, causing this bone also to rock forward. The upper end of the premaxilla, although harnessed
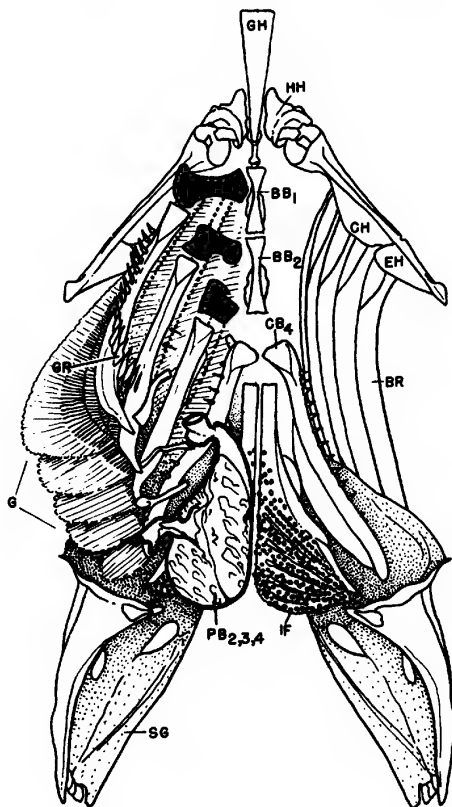

Fig. 12. Pharyngobranchial apparatus and shoulder girdle of the cyprinodontoid *Xiphophorus helleri* Heckel, dorsal view. Hypobranchials in solid black. Pharyngobranchials heavily outlined. The right first three arches are removed to show the branchiostegal rays below. Compare with figures 13 and 14.

to the rostrum by rather flexible ligaments, is incapable of more than the slightest movement, so that during the forward excursion of the lower arm of the premaxilla in response to maxillary pressure, the upper end of the premaxilla remains essentially in place. These jaw movements apparently are accompanied as in other fishes by a great expansion of the branchial chamber which in amblyopsids is highly elastic. Hence,

opening of the mouth in these fishes probably results in a sudden very great increase in the orobranchial volume that would cause water, and presumably also small organisms, to be drawn toward the well-toothed jaws. (See discussion of feeding habits in Poulson, MS.) Such a device
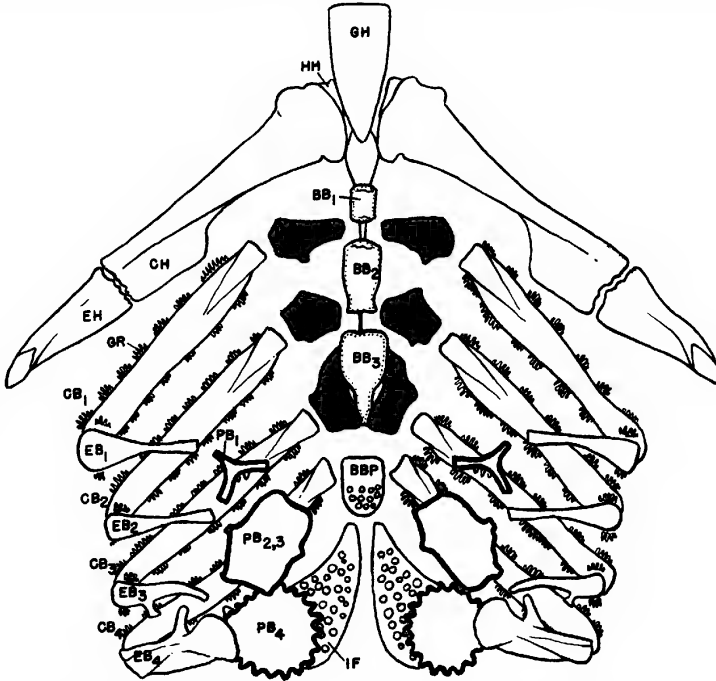

Fig. 13. Dorsal view, semidiagrammatic, of the pharyngobranchial apparatus of the amblyopsid *Amblyopsis spelaea* DeKay. Hypobranchials in solid black; pharyngobranchials heavily outlined. This pattern occurs also in *Aphredoderus*, *Percopsis*, and *Umbra*. In *Urophycis* the hypobranchials converge on a very short span of basibranchial ossification in the constricted copula, and the ceratohyal is less abruptly elevated; other details of the *Urophycis* branchial skeleton are like those of amblyopsids.

would appear to be advantageous for a nearly or completely sightless fish that must sense and quickly seize its prey.

This ability suddenly to augment the orobranchial volume seems to lie partly in a capacity to develop a very large tubular gape by driving the maxilla forward almost to the vertical position. In fishes generally the capability of forming a nearly circular aspect of the widely opened mouth has evolved many times independently. In numerous instances it has been achieved by the formation of a membranous wall that is stretched

between the upper and lower jaw or by the intrusion of the lower arm of the premaxilla into the gape. In certain clupeoids (e.g., *Opisthonema*) the maxillae are capable of rocking forward to a great extent to form the lateral boundaries of the roughly circular gape, which is true also of the amblyopsids. In amblyopsids, however, the premaxilla has functionally replaced the maxilla as the biting surface, and it is carried passively forward into the gape by maxillary movements of large amplitude.

The extent to which the lower arm of the maxilla can rock forward in these fishes is related to the unusual condition of the jaw muscles mentioned above. It is characterized by the loss (in *Chologaster cornuta*) or severe reduction of the external division (A_1) of this muscle and its liga-
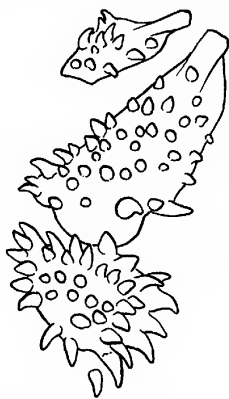
FIG. 14. Upper pharyngeal bones of *Aphredoderus sayanus* (Gilliams), ventral view, anterior up. Compare with figure 13.

mentous contact with the lower arm of the maxilla. The regulation of maxillary position is effected, however, by the levator maxillae superioris that extends upward along the palatopterygoid to the upper portion of the inner posterior face of the maxilla (fig. 6A). As is usual in fishes, the A_2A_3 division of the adductor mandibulae controls the raising of the mandible. The above-described condition of the jaw muscles has also been newly identified in the percopsids *Percopsis omiscomaycus* (fig. 6B) and *P. trans-montana*, the gadids *Urophycis floridanus*, *Microgadus proximus* (fig. 7), and *M. tomcod*, and in the ophidioids *Ophidion holbrooki* and *Monomitopus agassizi* (fig. 8).

Functionally, the reduction or loss of the external division of the adductor mandibulae muscle, and the disappearance or obsolescence of the ligament or tendon to the maxilla, mean that the lower maxillary arm can swing forward without being restrained from behind; it is limited

in its forward excursion only by the nature of its attachments to the mandible. In *Aphredoderus* and amblyopsids, and also in some gadids and ophidioids, the maxillae are capable of being forced forward to the upright position to form the walls of an oval or circular opening when the
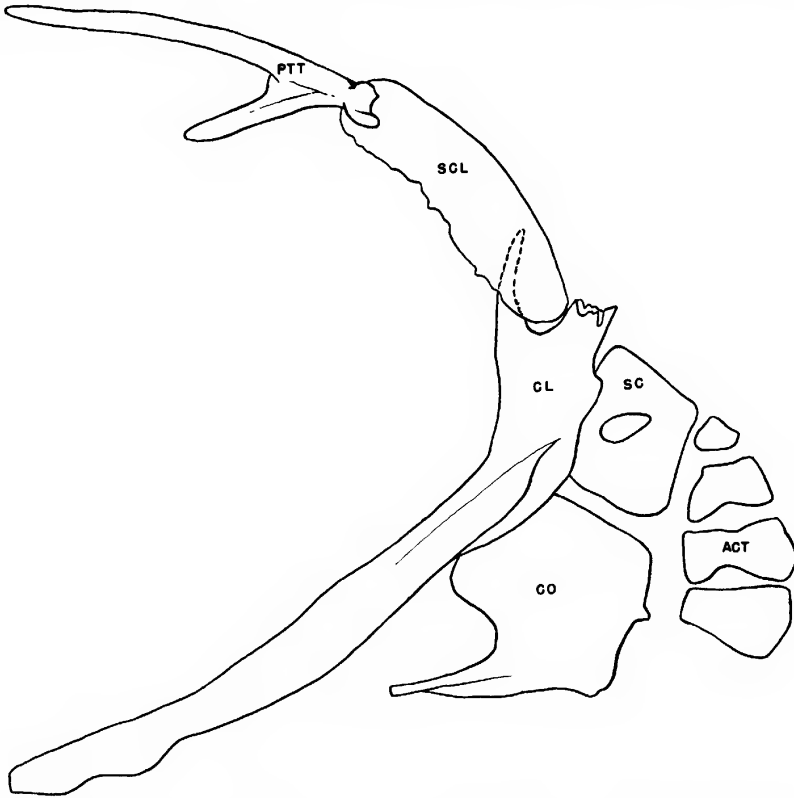

FIG. 15. Shoulder girdle of *Chologaster agassizi* Putnam. Compare with shoulder girdle in figure 11.

mouth is fully extended (figs. 8, 9). In some amblyopsids and in *Aphredoderus* the bending to which the premaxillary arm is subjected at this time appears to be compensated for by the flexibility of its segmental structure (figs. 4A, 10).

In a consideration of the origin of this mechanism, it should be noted that the external division of the adductor mandibulae muscle and its ligamentous attachment to the maxilla are not wholly lost, except in some species of amblyopsids and in *Aphredoderus*, of the fishes examined. The condition, therefore, appears to have been secondarily derived from a

mechanism of the percoid type in which A_1 is well developed and plays a role in moving the maxilla (see Schaeffer and Rosen, 1961, pp. 201–203). The presence of a levator maxillae superioris muscle to the maxilla has not been described as such in a percoid, although the tendon t.a$_3$mx of *Scomber* may represent the remains of this muscle, and Dietz (1914, 1921) and Takahasi (1925) illustrated a muscle here identified as lms[3,4] in a variety of fishes, including carangids and cyclopterids. Many features of the head skeleton of amblyopsids, percopsiforms, gadiforms, and ophidioids are, however, distinctly percoid, for example, the premaxillary
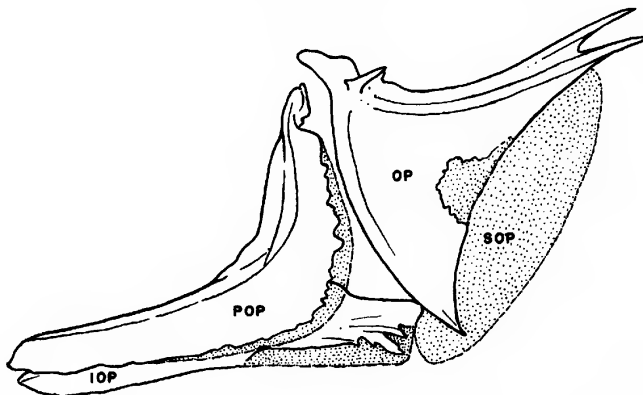
Fig. 16. Opercular apparatus of *Typhlichthys subterraneus* Girard. A bony subopercle could not be detected in the material at hand; the dashed line enclosing sop indicates the limits of a cartilaginous plate in the subopercular position. In *Percopsis omiscomaycus* the subopercular ossification is scarcely developed. In *Chologaster cornuta* it is large and well ossified.

processes, the upper jaw ligaments, the branchiostegal plan, and the opercular apparatus. Nevertheless, it is clear that the presence of a well-developed levator maxillae muscle in these fishes may represent the retention of a primitive actinopterygian feature. Eaton remarked that some features of the muscles of cods ". . . look suspiciously like archaic features, present, so far as known, in no other teleosts." Berg (1940) was ". . . inclined to regard the Gadiformes as a lowly organized order, derived from forms allied to Pachycormidae, probably at the end of the Cretaceous." Some of the osteological details of cods, especially the extremely large "opisthotic" (= intercalar), on which Berg based this statement, are present also in the Amblyopsidae.

Osteological and functional differences between amblyopsids and cyprinodontoids appear to warrant the idea here advocated that the
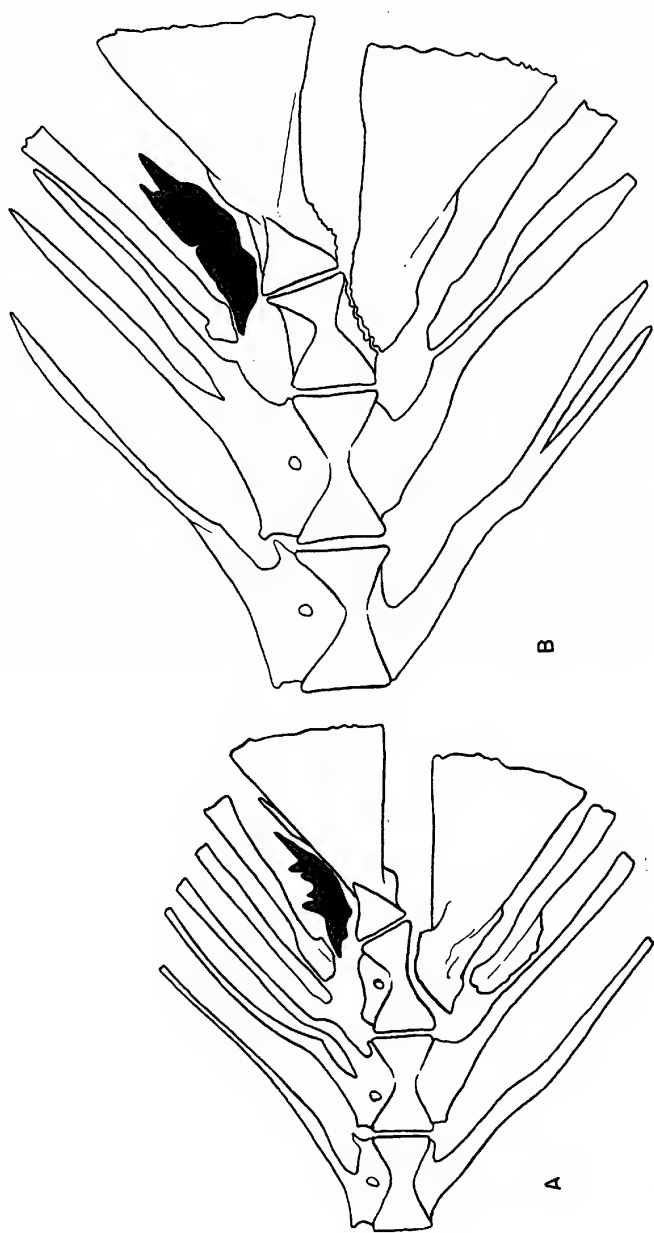
Fig. 17. Caudal skeletons. A. *Amblyopsis spelaea* DeKay. B. *Chologaster agassizi* Putnam. Woods and Inger (1957) state that the vertebrae are not turned up in *Amblyopsis rosae* (Eigenmann) and *Chologaster cornuta* Agassiz. Uroneural in solid black.
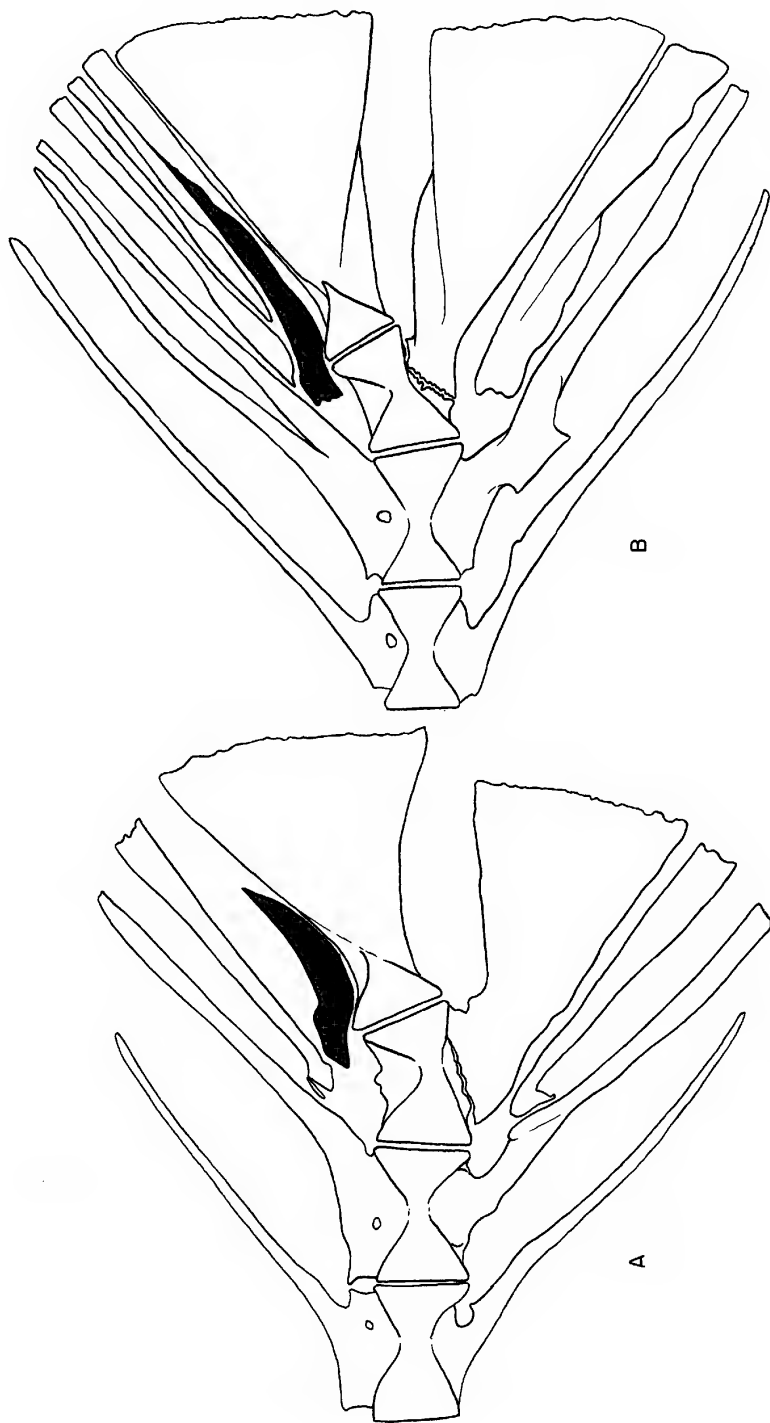
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Fig. 18. Caudal skeletons. A. *Typhlichthys subterraneus* Girard. B. *Aphredoderus sayanus* (Gilliams). Uroneural in solid black.
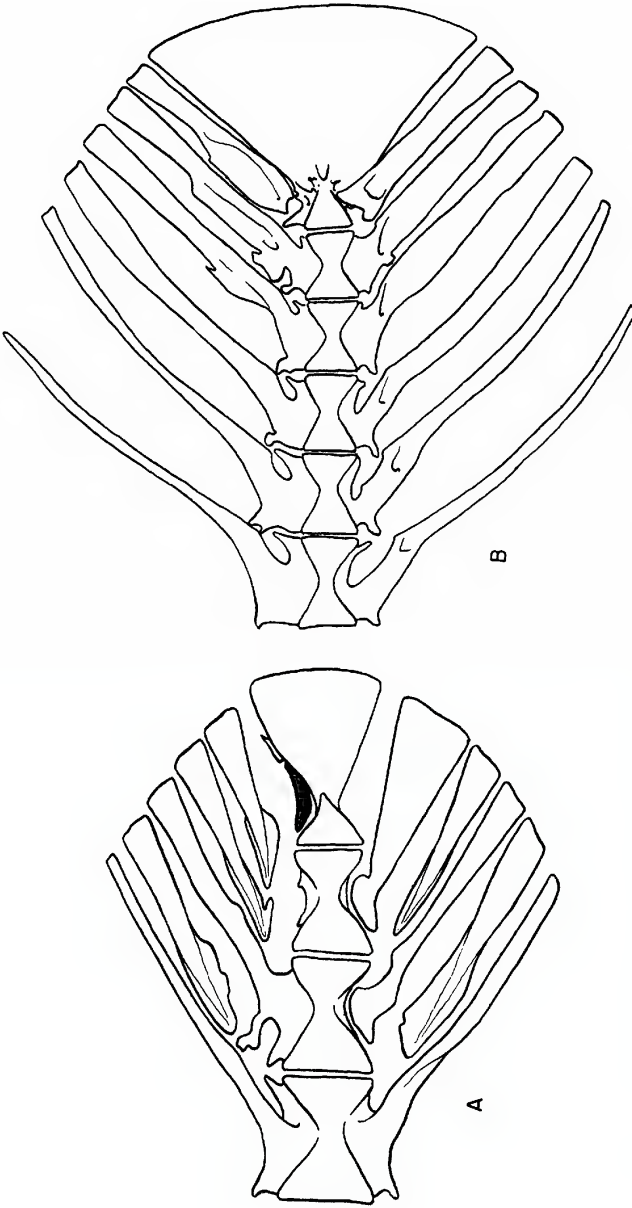
FIG. 19. Caudal skeletons. A. *Urophycis floridanus* (Bean and Dresel). B. *Fundulus confluentus* Goode and Bean. Uroneural in solid black.

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Amblyopsidae must be removed from the Cyprinodontiformes and placed elsewhere in the teleost assemblage. The also impressive number of similarities between these fishes and the pirate-perch, *Aphredoderus*, does not, however, provide an equally firm notion of their true affinities. The uncertainty of their actual relationships resides in the possibility that at
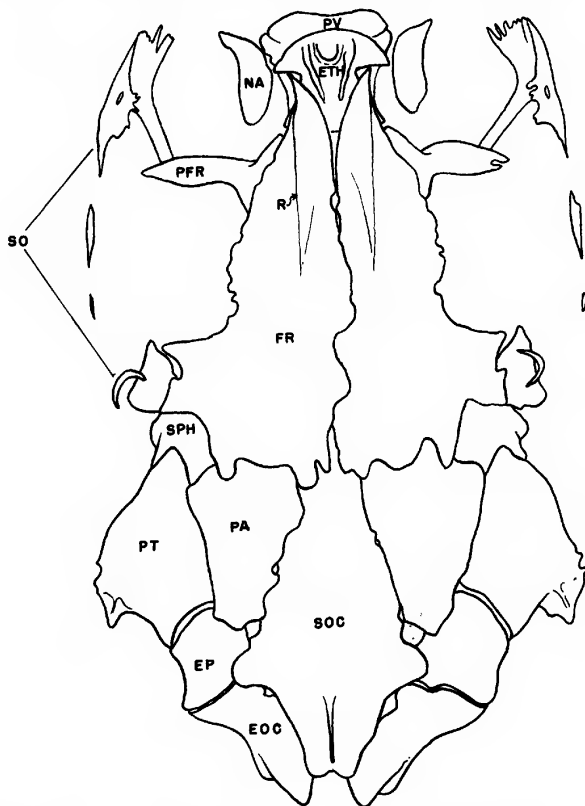

FIG. 20. Dorsicranium of *Chologaster agassizi* Putnam. The large areas of supra-occipital and exoccipital visible in *Chologaster* result from flattening of the occipital region. Note unpaired supraoccipital crest, orientation of parietals, presence of suborbital bones, and form of preorbital member of suborbital series.

least some of the features common to amblyopsids and *Aphredoderus* may be rather generally distributed among teleosts. Certain of these features are noted above in percopsids, gadids, and ophidioids. Still others may occur in additional groups. The bones of the jaw suspension, for example, are notably alike in amblyopsids, *Aphredoderus*, and the esocoid *Umbra* (figs. 5A, B, and 10). The amblyopsid-aphredoderid pharyngobranchial

apparatus and shoulder girdle are sufficiently generalized that one may expect to find them also represented in other groups (figs. 13–15).

In general, amblyopsids can be characterized as possessing some primitive and some progressive percoid-like features. Among the progressive ones are the development of a complex premaxilla with palatine
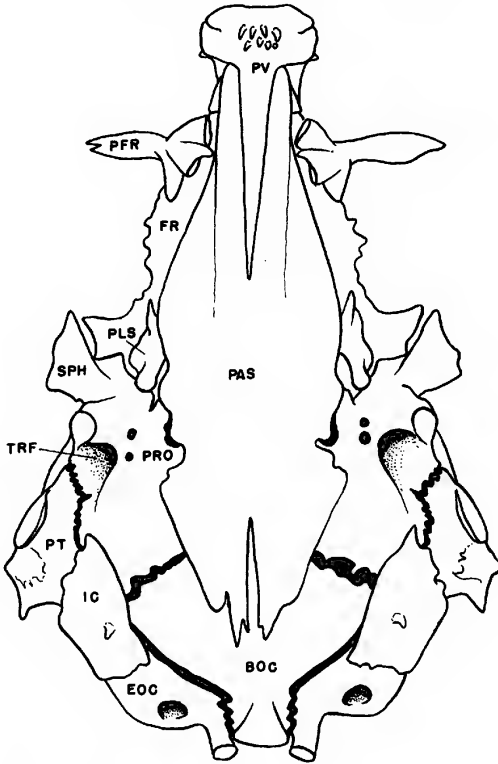

FIG. 21. Basicranium of *Chologaster agassizi* Putnam. Compare basicranial foramina with those in figure 2B.

and maxillary ligamentous connections, the exclusion of the maxilla from the gape, an abruptly elevated ceratohyal and six branchiostegal rays, and opercular spines (fig. 16). In addition to the peculiar jugular vent and frequently eyeless condition, they have an array of generalized and primitive features that includes a well-developed section of what may be the levator maxillae superioris muscle, abdominal pelvics (when present), no fin spines, an upturned asymmetrical caudal skeleton (figs. 17A, B, and 18A), a very large intercalar (fig. 21), and three separate toothed pharyngobranchials (fig. 13).

The present problem is to weigh the numerous specific points of similarity between amblyopsids and *Aphredoderus* (a form also with a mosaic of primitive and progressive elements)—particularly the specializations of the jaw muscles, upper jaw structure, hyoid and branchial apparatus, caudal skeleton (see also Gosline, 1961), and position of the
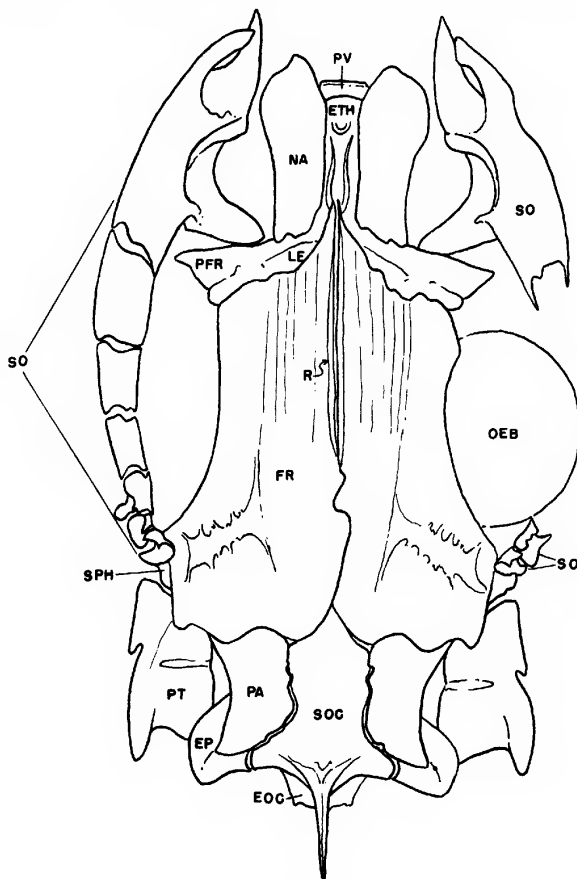

Fɪɢ. 22. Dorsicranium of *Percopsis omiscomaycus* (Walbaum). The cranial patterns of *Aphredoderus* and *Urophycis* are like those of *Percopsis*.

vent—against the known differences. For example, in *Aphredoderus* but not amblyopsids the scales are ctenoid, the pelvic fins have a thoracic insertion, and the anterior dorsal, pelvic, and anal fin rays are spinous. Ctenoid scales, however, are widely distributed among teleosts, and there is some indication that the scales may once have been ctenoid in *Cholo-gaster* (fig. 23). Moreover, the ctenoid scales of *Aphredoderus* are of a

unique type, according to Hubbs and Lagler (1949). The taxonomic significance of a thoracic insertion of the pelvic fins also is debatable, for pelvic fins have tended to shift forward in many unrelated groups. With regard to the prominent fin spines, C. L. Smith and R. M. Bailey recently pointed out to the author that the spines of *Aphredoderus* are variable in number, and they frequently have one or more joints near the tip, which implies a degree of hypocrisy in their spinous nature. Ginsburg (1953) previously provided evidence which casts doubt on the fundamental difference between spines and rays. Ginsburg showed that the third anal fin spine of *Pontinus longispinis* may be flexible and partly jointed for some distance at its distal end. In slightly larger specimens it is rigid and unsegmented. He commented: "This developmental phenomenon was heretofore well known in the species of *Mugil*. I have also observed it in the

FIG. 23. Scales as seen *in situ* on the flank of *Chologaster agassizi* Putnam. The bead-like formations on the posterior margin of the scales are claimed by Woods and Inger (1957) to be circulae interrupted by secondary radii. They are, however, in position to be obsolescent ctenii.

family Haemulonidae [Pomadasyidae], in the species of *Orthopristes* [*sic*], *Haemulon*, and *Bathystoma*. This noteworthy development, therefore, seems to be widespread in fishes. As the number of anal spines, 1, 2, or 3, is sometimes used as a family character, it is of interest to know that it depends on ontogenetic development in families of fishes which are otherwise widely divergent in the scheme of classification."

In addition, T. L. Poulson called to the present writer's attention differences between the cave fishes and pirate-perch in the structure of the endolymphatic system, but such differences as appear could be accounted for by the unusual degree of flattening posteriorly in the amblyopsid cranium (figs. 20, 21).

The differences between amblyopsids and aphredoderids are in some ways no greater than those that distinguish aphredoderids from percopsids as these two families are currently separated in the Percopsiformes. In *Percopsis*, for example, the vent is normal in position, and an adipose fin is present, as has previously been noted by Regan (1911a). Other features

of percopsids not found in aphredoderids involve principally the structure of the premaxilla (fig. 24A, B) and palatine (which in *P. omiscomaycus* is quite short and edentulous), the retention of a remnant of the external division of the adductor mandibulae muscle, the lobed caudal fin, and the lower number of dorsal fin spines. Percopsids do, of course, possess the basic amblyopsid-aphredoderid type of jaw muscles and caudal skeleton.
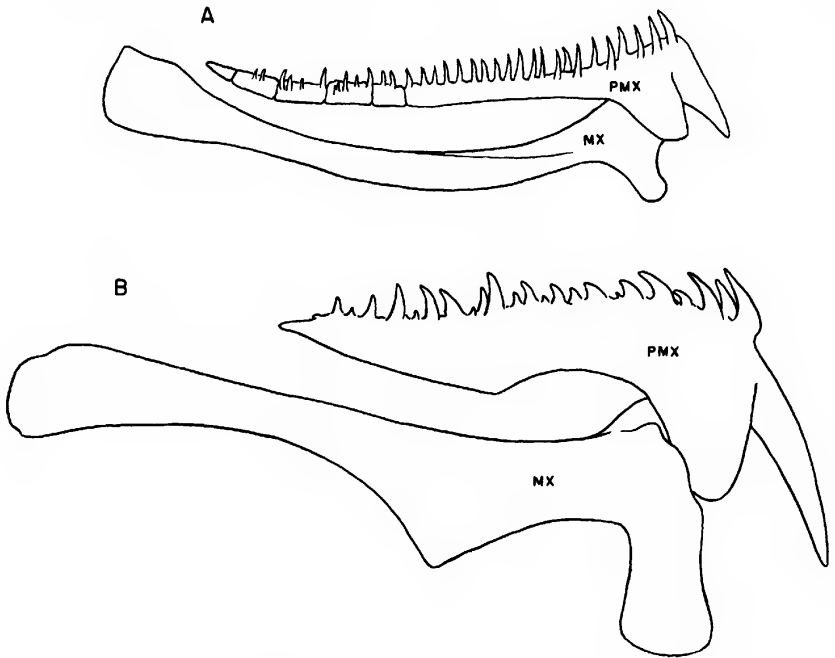

FIG. 24. Dorsal views of left upper jaw bones. A. *Aphredoderus sayanus* (Gilliams). B. *Percopsis omiscomaycus* (Walbaum).

The present intention is to suggest a new alignment for the amblyopsid fishes as a means of underscoring their many distinctive features. It is recommended that the Amblyopsidae be relegated provisionally to an order, the Amblyopsiformes,[1] adjoining the Percopsiformes in current classification. Parenthetically, the resemblances between these two orders and the gadiforms and ophidioids suggest the existence of a phyletic

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[1] The name "Amblyopsiformes" was used by Goodrich (1930) as a subordinal equivalent of the Microcyprini, and more recently by Bertin and Arambourg (1958), without explanation, for the Amblyopsidae alone. The taxonomic isolation of the Amblyopsidae leaves the Cyprinodontoidei equivalent in scope to the Cyprinodontiformes.

assemblage, the members of which have attained different levels of structural organization. Also noteworthy is the fact that each of these groups includes some forms that inhabit dim or lightless environments. Finally, it seems only remotely possible that amblyopsiforms and percopsiforms should have attained such remarkable similarities without benefit of a common, though distant, ancestor.

SUMMARY

During the past half century, the order Cyprinodontiformes (= Microcyprini, Cyprinodontes, Cyprinodontida) was divided into two major groups, the Cyprinodontoidei (typical killifishes) and the Amblyopsoidei (North American cave fishes). Evidence is now presented indicating that these two groups of fishes have been improperly associated taxonomically. On the basis of numerous osteological, myological, and functional features, the amblyopsids are shown to resemble *Aphredoderus* in considerable detail. Features that appear to unite the amblyopsids and *Aphredoderus* are found also in *Percopsis*. Many, though by no means all, of the characters common to amblyopsids and percopsiforms are identified in three gadids, a brotulid, and an ophidiid. The provisional assignment of the Amblyopsidae to a separate order, the Amblyopsiformes, adjoining the Percopsiformes in current classification, is proposed. It is noted parenthetically that the resemblances between these two orders and the Gadiformes and Ophidioidei suggest the existence of a phyletic assemblage in which each group represents a different level of structural organization. Attention is called to the fact that the Amblyopsiformes, Percopsiformes, Gadiformes, and Ophidioidei include forms characteristically inhabiting dim or lightless environments.

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